



W&M ScholarWorks

VIMS Articles

Virginia Institute of Marine Science

2000

Restoring The Oyster Reef Communities In The Chesapeake Bay: A Commentary

Roger L. Mann

Virginia Institute of Marine Science

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Marine Biology Commons](#)

Recommended Citation

Mann, Roger L., "Restoring The Oyster Reef Communities In The Chesapeake Bay: A Commentary" (2000).
VIMS Articles. 482.

<https://scholarworks.wm.edu/vimsarticles/482>

This Article is brought to you for free and open access by the Virginia Institute of Marine Science at W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

RESTORING THE OYSTER REEF COMMUNITIES IN THE CHESAPEAKE BAY: A COMMENTARY

ROGER MANN

Virginia Institute of Marine Science
College of William and Mary
P. O. Box 1346
Gloucester Point, Virginia 23062

ABSTRACT Restoration of the oyster *Crassostrea virginica* resource to the Chesapeake Bay is a widely supported goal. This manuscript explores the questions of why, how, and in what time frame this should be attempted. Restoration goals based simply on support of a commercial fishery fail to address the role of the oyster as a cornerstone species within the Chesapeake Bay and should only be considered in the context of a long-term sustainable fishery exploitation. The argument is proffered that a restored resource sustaining a fishery at the historical harvest level is unrealistic, because: (1) harvest probably exceeded biological production for much of the recorded history of exploitation; and (2) maximum production, a desired end for fishery support, occurs at approximately half the maximum (virgin, unexploited) biomass, and, thus, can only be achieved with disruption of the virgin complex community structure. Thus, the direct harvest economic value of a fishery based on a restored resource will not reach historical levels if there is an accompanying goal of long-term community development that is self-sustaining in the absence of restoration effort. The role of the oyster as a cornerstone organism and the pivotal link in benthic-pelagic coupling is examined in the context of current and projected watershed management problems, including agricultural and urban development with associated nutrient and sediment erosion issues, in the entire Chesapeake Bay watershed. Restoration efforts to date have focused on rebuilding three-dimensional reef structures, often with subsequent oyster broodstock enhancement, in predominantly small estuaries with retentive circulation to provide demonstration of increased resultant recruitment. Such examples are used to increase public awareness of the success of restoration processes and increase long-term participation in such programs by schools, nonprofit and civic organizations, and commercial and recreational fishing groups.

KEY WORDS: oysters, *Crassostrea virginica*, Chesapeake Bay, reefs, restoration, watershed, management, benthic-pelagic coupling

DEFINING THE PROBLEM, PART 1: BIOLOGY, ECONOMICS, PERCEPTION, AND TIME FRAMES

The Chesapeake Bay has a history related to the eastern oyster *Crassostrea virginica*. Much of the biology of the bay over the past 10,000 years is arguably dependent on the reef-forming habit of this cornerstone species. Oysters were an important food source to pre-Colonial native populations, were quickly recognized for their value after Colonial settlement, became the center of a national and international trade before the end of the 19th century, and remained a substantial component of the Middle Atlantic economy through the first six decades of the 20th century. The past four decades have been marked by the appearance and continued destructive effects of two disease vectors, *Haplosporidium nelsoni*, commonly known as MSX, and *Perkinsus marinus*, commonly known as Dermo, in the higher salinity regions of the bay.

When considered together with the cumulative effect of many decades of overfishing and environmental decay, the result is a sadly depleted oyster resource in the Chesapeake Bay. Although consensus is growing that attempted restoration of this resource is a noble and worthwhile cause, the task before us is to ask why, how, and in what time frame this should be attempted.

Given that the oyster has long supported a commercial fishery in the Chesapeake Bay, a logical first question is "Should the revitalization of the oyster fishery be the prime motivation for restoration of the oyster populations in the bay?" Such a question has a number of inherent qualifiers. Fisheries utilize a biological resource to optimize or maximize economic or societal return. Restoration of the resource for this prime purpose would be in a form that optimizes harvest over a defined time frame—a form that may not, as is discussed later, be considered best for optimizing ecological complexity and stability. Economies have time horizons

of importance, thus any restoration effort must respect and be responsive to this time frame. The societal component must be equally addressed in that restoration to enhance an economic contribution to a thriving economy must be responsive in a politically expedient time frame; that is, efforts must create a strong public perception of improvement in the face of multiple competing needs for public funding. Economy, perception, and time frame, in addition to biology, become important factors in setting fishery restoration goals.

What might be reasonable goals for a fishery-driven restoration program? The recent and current oyster fishery in the Chesapeake Bay has several components. These must be distinguished from the oyster industry, which includes processing of oysters originating in regions other than the bay. In Maryland, there currently exists an active public fishery prosecuted by watermen who purchase licenses to harvest oysters from resources in regions held in public trust by the State of Maryland. The harvest from this fishery typically exceeds its Virginia counterpart by a very substantial amount. However, this harvest is "underwritten" both by substantial public funds and by the continuing effort by the Maryland Department of Natural Resources to plant shell substrate in selected regions in advance of seasonal oyster settlement (spatfall) and to move the resultant "seed" to regions for optimal growth in the face of potential disease pressure. This program is arguably very responsive to a fishery need; the long-term issue of resource restoration is not a prime mission of the program. A similar program of shell deployment and subsequent "seed" movement on grounds retained in public trust has also been pursued in Virginia. The incremental impacts of disease have reduced the effectiveness of the Virginia program in supporting a continuing industry, and current landings from the fishery are at an all-time low. As in Maryland, the focus of this "plant and move seed" program has been short term, with

no statement on long-term restoration. Virginia also allows leasing of "suboptimal" bottom adjacent to public grounds. These regions sustain a very substantial fishery harvest essentially in grow-out of "seed" oysters but are operated on a put-and-take basis with a 2–3 year growth period. Again, these are strictly for-profit operations by private individuals or corporations with no restoration goal (see Haven et al. 1981a,b). Such efforts have all but disappeared in the past decade as a result of the continued incidence of disease. The losses accompanying the fishery's decline since the major onset of disease have had a subtle societal impact that has generated considerable public debate and, in some instances, sympathy. Commercial fishermen are among the few remaining "hunter-gatherers" in modern society, and their visible demise in the Chesapeake Bay oyster fisheries is viewed (perhaps unrealistically) as a loss of individuals who operate with large amounts of personal freedom in a society that pays little attention to that same personal freedom. A reasonable goal from an economic position would be the restoration of a fishery resource to support a predisease level of harvest, typically several millions of bushels per year for Maryland and Virginia combined, with some enhancement of the societal role supported by the fishery.

Is a fishery-driven restoration to sustain a predisease level of harvest a reasonable goal for ecological restoration? Arguably, no. An examination of the historical fishery harvest finds that the harvest was much greater before the turn of the century. The combined harvest of oysters in 1865 by Maryland and Virginia alone was approximately 17 million bushels (Hargis and Haven 1988)—enough oysters to bury a football field to the depth of 656 feet! This is an astonishing amount given the primitive dredging and tonging techniques employed, but it illustrates simply the level of fishing pressure employed in the latter half of the 19th century. We know from the works of Ingersoll (1881), Brookes (1891), and others that a century ago strong concerns about overfishing and its eventual impact were expressed to regulatory bodies. Although these concerns stimulated a limited regulatory effort, and the surveys of Winslow in Maryland and Baylor (1894) in Virginia to define the extent of the public resource, the comments did little to abate the revisiting of the "tragedy of the commons." The important issue to this commentary, however, is that the enormous removals of oysters had proportionate impact on the biology of the oyster in the bay. Neither as part of the process of oyster harvesting nor as part of the discussion (minimal for much of the time) on resource management was a formal assessment of stock size or estimate of productivity ever made. However, the fundamental understanding of the importance of these processes was already central to the discussion of marine finfish stocks on both sides of the Atlantic before the turn of the century, as demonstrated by the work of Spencer Baird, G.O. Sars, and their peers. Although very large and obviously old oysters were still abundant in the bay during the heyday (1860s) of harvest (de Broca 1865), we also know from navigation charts prepared by the U.S. Navy before the turn of the century, that three-dimensional oyster reef structures were exposed only at low tide in many regions of the bay. These reefs gradually became permanently subtidal with continued wholesale mining of the resource for both food and industrial (chicken grit to limestone to road surfacing material) purposes. Indeed, gradual submergence of the reefs could not be ascribed to sea level rise!

Proceeding further back in time, we move from the period of highest harvest in the latter half of the 19th century to the period of Colonial settlement, when intertidal oyster reefs were abundant

and notable features of the bay. It is this presettlement era that illustrates the most defensible target for restoration goals. Throughout the preceding discussion there has been frequent mention of fishery harvest, but purposely not of biological production. In a well-managed, economically exploited resource, the harvest does not exceed production. Given the lack of assessment and productivity data, a definitive temporal analysis of the post-Colonial settlement harvest in excess of productivity is not possible. However, we do know that the cumulative result has been the removal in less than 400 years of complex reefs that developed over a 10,000-year period, beginning with the inundation of the bay in the current postglacial warming period.

Acceptance of the tenet that cumulative harvest was clearly in excess of cumulative production places the question of restoration for fishery harvest in a new light. The projection of a restored resource being able to sustain a fishery at the historical harvest level is unrealistic because: (1) harvest probably exceeded biological production for much of the recorded history of exploitation; and (1) maximum production, a desired end for fishery support, occurs at approximately half the maximum (virgin unexploited) biomass (as defined in Applegate et al. 1998, Restrepo et al. 1998) and, thus, can only be achieved with disruption of the virgin complex community structure. Indeed, the direct harvest economic value of a fishery based on a restored resource will not reach historical levels unless there is an accompanying goal of long-term community development that is self-sustaining in the absence of restoration effort. It is, therefore, unreasonable to consider a restoration effort for oyster fishery support purposes alone. This conclusion prompts the question, "If the goal is not just the fishery harvest, what end point should restoration goals seek to achieve?" I argue that oyster restoration should be viewed as the re-establishment of (one of several) cornerstones in an ecosystem.

DEFINING THE PROBLEM, PART 2: A CORNERSTONE IN THE ECOSYSTEM

The reason oysters are the focus of shellfish restoration in Chesapeake Bay is their value as a cornerstone species in the bay. Oysters are a major benthic-pelagic coupler; one that supports a diverse food web in higher trophic levels and, as an added bonus, is the basis of a commercial fishery of secondary importance to the food web structure.

How big is the baywide problem? Enormous. The Chesapeake Bay is 298 km long (185 miles), has a surface area of 8,484 km² (3277 sq. miles), and has a volume of 71.5×10^9 m³ (Cronin and Pritchard 1975). Within this context the biology of the oyster deserves attention. Oysters are gregarious and long-lived (therefore, large) in a pristine environment. Spawning efficiency is maximized by simultaneous gamete release in these dense aggregations (see studies by Levitan 1991, Levitan et al. 1991, 1992 for sessile benthic organisms, sea urchins, in spawning and fertilization efficiency). Individual fecundity increases with size (Thompson et al. 1996 using data from Cox and Mann 1992), so dense aggregations of large animals should be a goal of restoration, because they help provide long-term stability through provision of larval forms. Dense aggregations grow in the third dimension (up) in the presence of adequate food. Multigeneration aggregate settlement creates three-dimensional structure as older animals die but remain as substrate for new recruits to the benthos. Three-dimensional structure would, therefore, seem to be a further defensible goal of restorative efforts.

The trophic role of oysters in the Chesapeake Bay and other similar systems has been well studied; therefore, quantitative arguments can be proffered: (1) to support the level of restoration; and (2) to estimate the trophic impact on both nutrient reduction through grazing and higher trophic production through support of enhanced food chains (see Newell 1988, Baird and Ulanowicz 1989, Ulanowicz and Tuttle 1992, for examples). An examination of these contributions underscores the need to consider oyster restoration not as a singular goal but as a component of a holistic approach to watershed management that includes land use practices and the subsequent impact of riverine input to water column processes throughout the bay and its subestuaries. Water column processes are then to be considered in the context of local habitat and benthos (including oyster reefs), progressing to include resident and seasonally migratory transient macrofauna. The complexity and size of the problem has, fortunately, received much attention. The NOAA and EPA Chesapeake Bay Program databases in addition to those of the U.S. Geological Survey (most of these are now available through the World Wide Web) are replete with useful information to guide the restoration plan. To reiterate, a restoration process must be placed in a time context. The changes in the original watershed from forested to a mix of urban, agriculture, and forest occurred over the period from Colonial times to the present; the projected population growth through 2020 within the watershed, especially the coastal regions of Maryland and Virginia, exceeds projected national growth rates. Increases in the human population within the watershed from the current 14 million to 16–18 million are within reason in this time period. Attempts to plan and control growth within the watershed are and will continue to be both politically charged and difficult to resolve. Unfortunately, historical precedent illustrates a general lack of resolve in this country to limit growth and exploitation effectively. Therefore, land use and runoff issues associated with these projections will raise discussion of freshwater diversion, use, re-use, discharge, groundwater use and contamination, and saltwater intrusion. Every item on this list directly affects nutrient and sediment inputs to the bay and will tax the capabilities of recent amelioration strategies to reduce negative effects.

The biological consequences of increased inputs of nutrient and particulate material to the bay watershed are well understood. Nutrients stimulate productivity in excess of the grazing capacity of the resident filter feeders, notably the benthic filter feeders. Sediment loads that inhibit the filtering process exacerbate the situation. With limited grazing, eutrophication is inevitable. Sediment loads similarly inhibit extension of submerged aquatic vegetation (SAV) by limiting light penetration of the water column. The complex nature of the restoration problem is well illustrated by consideration of a two-species interaction: that of oysters with SAV. On a riverwide scale the presence of multiple reef systems with vertical relief in otherwise open bodies of water, like much of the Chesapeake Bay, reduces fetch and, hence, wind-driven resuspension of particulate material in the water column. The presence of fringing reefs reduces sediment input from shoreline erosion. At a smaller scale, filter feeding by oysters reduces water column loads of sediment and plankton; thereby, increasing light penetration and increasing SAV growth. Bottom stabilization by SAV increases water quality; thereby, encouraging a positive feedback loop to oyster growth. There is nonlinearity in this feedback: when the suspended sediment load increases above a certain level, SAV growth essentially ceases, and the response of the oyster filter-feeding rate to sediment load approximates a parabola. Thus, al-

though publicly stated goals of 40% nutrient reduction in nutrient input are laudable, they must be accompanied by a critical reduction in sediment load to allow SAV growth and the oyster–SAV positive feedback interaction to develop. This multifaceted problem of both elevated nutrients and sediments is notable in areas that once supported abundant oyster populations—the James, York, and Rappahannock rivers, and Pocomoke–Tangier Sound—and are given critical status on current Chesapeake Bay Program and EPA World Wide Web sites. Proceeding above a “simple” two-species interaction, Lenihan and Peterson (1998) underscore the sensitivity of the multispecies interaction on reefs to multiple environmental factors.

The enormity of the potential restoration effort and its primary goal is easily recognized. Is there a logical recovery protocol? I argue, yes. The unique aspects of the biology of the oyster in the bay that must be exploited to facilitate restoration are known: high density and a three-dimensional structure in a location where filter feeding will not be overwhelmed initially by local water quality conditions. In Virginia, these aspects have been used to guide the choice of location for early restoration efforts. A critical issue from both the biological and political view is the choice of sites. Sites must be selected such that the impact of the effort is visible in a short (months to a small number of years) time frame; that is, the signal from the restoration effort must be “visible” above the natural variability or “noise” in the target system. Thus, there is a need to match scale of effort with goals. Attempting wholesale restoration of large river systems at the outset is clearly not viable for either cost or biological considerations, but there are many smaller parts of candidate systems that are attractive. Using such resources as the Baylor ground maps (1894), natural reef “footprints” have been identified that can be cleaned of remaining oysters and used as a base to build three-dimensional structure.

Under the guidance of the Shellfish Replenishment Program at the Virginia Marine Resources Commission, a reef-based restoration effort was initiated in the Piankatank River in 1993 with construction of a single reef at Palace Bar. No broodstock addition was effected at the site. Construction is described in Bartol and Mann (1997). Since its construction, this site has been studied intensively in terms of oyster recruitment and growth (Bartol and Mann 1997, in press, Mann and Wesson unpublished data), disease progression in recruited oysters (Volety et al. 2000, this issue), and development of associated fish and benthic communities (Harding 1999, Harding and Mann 1999, 2000). A contrasting approach was employed in the Great Wicomico River in 1996 (Southworth and Mann 1998). The success of this effort warrants description as a model for restoration programs. The Great Wicomico River is a small, trap-type estuary on the western shore of the Chesapeake Bay that once supported substantial oyster populations. The combined effects of Tropical Storm Agnes in 1972 and subsequent disease mortalities related to *Perkinsus marinus* and *Haplosporidium nelsoni* essentially eliminated these populations. Oyster broodstock enhancement was initiated in June 1996 by the construction of a three-dimensional intertidal reef with oyster shell, followed by “seeding” of the reef in December 1996 with high densities of large oysters from disease-challenged populations in Pocomoke and Tangier Sound. (In these donor locations, the extant oyster population density is too low to effect reasonable probability of fertilization success and subsequent recruitment.) Calculations of estimated fecundity of the resultant reef population suggested that oyster egg production from this source were within an

order of magnitude of total egg production in the Great Wicomico River before Tropical Storm Agnes. Field studies in 1997 indicated spawning by reef oysters from July through September; whereas, plankton tows recorded oyster larval concentrations as high as $37,362 \pm 4,380$ larvae/m³ (on June 23)! Such values are orders of magnitude higher than those typically recorded for Virginia subestuaries of Chesapeake Bay in the past three decades and strongly endorse a premise of aggregating large oysters to increase fertilization efficiency. Drifter studies suggest strong local retention of larvae, a suggestion reinforced by marked increases in local oyster spatfall on both shell string collectors and bottom substrate in comparison to years before 1997. Although disease was evident in the population—*Perkinsus* prevalence increased from 32% in June to 100% in July, and intensity increased from June to September—the effort demonstrated that choosing locations where local circulation promotes larval retention combined with reef construction and broodstock enhancement may provide an accelerated method for oyster population restoration. Following the above observation in the Great Wicomico, two reef sites in the Piankatank have been added as part of the broodstock enhancement program using large oysters collected from high salinity regions of the bay where disease pressure remains high. Similar efforts are underway in two small tributaries of the Potomac River (the Coan and Yeocomico), the Elizabeth River, Pungoteague Creek on the bay side of the Eastern Shore of Virginia, and Lynnhaven Bay on the south shore of the Chesapeake Bay mouth. In addition, reefs of various substrate types have been constructed at Fisherman's Island at the southern tip of the Eastern Shore of Virginia and are the site of continuing intense study by Luckenbach and collaborators based at the Virginia Institute of Marine Science Wachapreague Laboratory.

Although there is a clear generic component to these individual efforts of small reefs in small systems, each site is unique along a salinity cline within Virginia waters. They represent a mosaic of habitat types with differing environmental values in both biology and physical structure. Such unique aspects of each reef system are examined further by Breitburg et al. (2000, this volume). Provision of complex physical habitat structure provides opportunity for recruitment by species other than oysters as demonstrated by Breitburg et al. (1995), Breitburg (1999), Harding and Mann (1999, 2000), Nestlerode and Luckenbach (in press), and Coen and Luckenbach (in press). To date, the progression of increasing species richness and complexity in relation to presence or absence of "seeded" oyster broodstock has not been investigated, although it is reasonable to suggest that the presence of the latter accelerates development of the multitrophic community on and around the reefs.

The problem for proponents of reef restoration as a central mechanism to restore oyster resources is not so much the demonstration of biological recruitment in the field as the social and political recruitment of citizens to support such efforts on a long-term basis. Demonstration of "success" in field programs, such as the recruitment event associated with reef construction and broodstock "seeding" in the Great Wicomico River in 1997, provide a vehicle to educate the public and foster vested interest groups. The target audience here is broad, as demonstrated by success to date in developing partnerships, which is illustrated by the following examples. Established environmental nonprofit groups, such as the Chesapeake Bay Foundation, use their considerable resources and infrastructure to support reef efforts on a regional basis. In stark contrast to the "not in my back yard" mentality associated with

environmentally adverse programs, reefs are environmentally attractive structures that are desired "in my back yard." Consequently, local citizens groups sponsor reefs in their own "back yards" and school groups grow oysters to seed local reefs as part of the restoration effort. Currently lacking from this team is strong endorsement of both the commercial and recreational fishing communities in the bay. This is surprising, given the obvious long-term advantage to both, but probably reflects the immediacy of benefit that is required to attract these groups. Education is the avenue to forge this relationship, as demonstrated by the active support enjoyed by SAV restoration efforts from the fishing community. An integral part of this education must be the demonstration of the economic value of an ecological asset not just in terms of the commercial and recreational end product. It must be evident that that there is a cumulative positive impact of restored ecosystems in nutrient processing that is preferable to the current "single-payment option" exercised by some point-source nutrient abatement policies. The challenge remains to enjoin a broad citizen base in supporting ecological restoration on a broad base, understanding that they have vested interest as long-term investors in the watershed in which they communally reside with the Chesapeake Bay flora and fauna.

ACKNOWLEDGMENTS

This manuscript was presented as a plenary presentation commentary at the Second International Conference on Shellfish Restoration, convened at Hilton Head, South Carolina, on November 19–21, 1998. This work of the author and collaborators described in this article was supported in part by the EPA Chesapeake Bay Program; the Commonwealth of Virginia, Department of Environmental Quality, Chesapeake Bay and Coastal Programs, and operating funds of the Virginia Institute of Marine Science. Partial support to the author during the period of manuscript preparation was provided by National Science Foundation Grant OCE-9810624. Support to present the manuscript at the Second International Conference on Shellfish Restoration was provided by the National Oceanic and Atmospheric Administration. These sources of support are gratefully acknowledged. I thank my colleagues, James Wesson, Mark L. Luckenbach, Ian Bartol, Juliana Harding, Melissa Southworth, Janet Nestlerode, Francis O'Beirn, and William J. Hargis, Jr., for many interesting discussions on reef biology and the Chesapeake Bay. This contribution is dedicated to William J. Hargis, Jr., who during both his years as director of the Virginia Institute of Marine Science and since retirement has argued tirelessly for oyster restoration in the Chesapeake Bay. Contribution number 2311 from the Virginia Institute of Marine Science.

LITERATURE CITED

- Applegate, A., S. Cadrin, J. Hoenig, C. Moore, S. Murawski & E. Pikitch. 1998. Evaluation of existing overfishing definitions and recommendations for new overfishing definitions to comply with the sustainable fisheries act. Final Report of the Overfishing Definition Review Panel to the Mid Atlantic Fishery Council. 179 pp.
- Baird, D. & R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay. *Ecol. Monogr.* 59:329–364.
- Bartol, I. & R. Mann. 1997. Small-scale settlement patterns of the oyster *Crassostrea virginica* on a constructed intertidal reef. *Bull. Mar. Sci.* 61(3):881–897.
- Bartol, I. & R. Mann. 1999. Growth and mortality of oysters (*Crassostrea virginica*) on constructed intertidal reefs: Effects of tidal height and substrate level. *J. Exp. Mar. Biol. Ecol.* 237:157–184.
- Baylor, J. B. 1894. Method of defining and locating natural oyster beds,

- rocks, and shoals. Oyster Records (pamphlets, one for each Tidewater, Virginia county that listed the precise boundaries of the Baylor Survey). Board of Fisheries of Virginia, Virginia.
- Breitburg, D. C. 1999. Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? pp. 239–250. *In*: M. W. Luckenbach, R. Mann and J. A. Wesson (eds.). Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Breitburg, D. L., L. Coen, M. L. Luckenbach, R. Mann, M. Posey & J. A. Wesson. 2000. Oyster reef restoration: Convergence of harvest and conservation strategies. *J. Shellfish Res.* (this issue)
- Breitburg, D. L., M. A. Palmer & T. Loher. 1995. Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. *Mar. Ecol. Prog. Ser.* 125:45–60.
- Brooks, W. K. 1891. The Oyster. re-issued. 1996 edition with a foreword by K.T. Paynter, Jr. The Johns Hopkins University Press, Baltimore, MD. 230 pp.
- Coen, L. & M. L. Luckenbach. in press. Developing success criteria and goals for evaluating shellfish habitat restoration: Ecological function or resource exploitation? *Ecol. Eng.*
- Cronin E. & D. W. Pritchard. 1975. Additional Statistics in the Dimensions of the Chesapeake Bay and Its Tributaries: Cross Section Widths and Segment Volumes per Meter Depth. Chesapeake Bay Institute Special Rept. 42. The John Hopkins University, Baltimore, MD.
- Cox, C. & R. Mann. 1992. Temporal and spatial changes in fecundity of oysters, *Crassostrea virginica* (Gmelin), in the James River, Virginia, U.S.A. *J. Shellfish Res.* 11(1):47–52.
- de Broca, P. 1865. Etude sur l'industrie huître des Etats-Unis, faite par ordre de S.E.M. le Comte de Chasse-loup Laubat, ministre de la marine et des colonies. Challamel aine, Paris. 266 pp. (English translation: On the oyster industries of the United States. Rept. Comm. U.S. Comm. Fish and Fisheries. 1873–1875: 271–319 {1876}).
- Harding, J. M. 1999. Selective feeding behavior of larval naked gobies (*Gobiosoma bosc*) and blennies (*Chasmodes bosquianus* and *Hypsoblennius hentzi*): preferences for bivalve veligers. *Mar. Ecol. Prog. Ser.* 179:145–153.
- Harding, J. M. & R. Mann. 1999. Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. *Bull. Mar. Sci.* 65(1): 289–300.
- Harding, J. M. & R. Mann. 2000. Naked goby (*Gobiosoma bosc*) and striped blenny (*Chasmodes bosquianus*) population dynamics around restored Chesapeake Bay oyster reefs. *Bull. Mar. Sci.* 66(1):29–45.
- Hargis, W. J., Jr. & D. S. Haven. 1988. The imperiled oyster industry of Virginia. VIMS Special Rept. 290 in Applied Marine Science and Ocean Engineering, Virginia Institute of Marine Science, Gloucester Point, Virginia. 130 pp.
- Haven, D. S., J. P. Whitcomb & P. Kendall. 1980a. The present and potential productivity of the Baylor Grounds in Virginia. VIMS Special Rept. 243 in Applied Marine Science and Ocean Engineering, Virginia Institute of Marine Science, Gloucester Point, Virginia. 154 pp.
- Haven, D. S., W. J. Hargis, Jr. & P. Kendall. 1981b. The oyster industry of Virginia: its status, problems, and promise. Special Papers in Marine Science 4. Virginia Institute of Marine Science, Gloucester Point, Virginia. 1024 pp.
- Ingersoll, E. 1881. The oyster industry. The History and Present Condition of the Fishery Industries: Tenth Census of the United States, Department of the Interior, Washington, DC. 251 pp.
- Lenihan, H. S. & C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol. Appl.* 8(1):128–140.
- Levitan, D. R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol. Bull.* 181:261–268.
- Levitan, D. R., M. A. Sewell & Fu-Shiang Chia. 1991. Kinetics of fertilization in the sea urchin *Strongylocentrotus franciscanus*: Interaction of gamete dilution, age, and contact time. *Biol. Bull.* 181:371–378.
- Levitan, D. R., M. A. Sewell & Fu-Shiang Chia. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology* 73(1):248–254.
- Nestlerode, J. A. & M. W. Luckenbach. in press. Trends in early community development and trophic links on constructed oyster reef. Abstract, Second International Conference on Shellfish Restoration. *J. Shellfish Res.*
- Newell, R. I. E. 1988. Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*? pp. 536–546. *In*: M. P. Lynch & E. C. Krome (eds.). Understanding the Estuary: Advances in Chesapeake Bay Research. Chesapeake Research Consortium, Publication 129 CBP/TRS 24/88, Gloucester Point, VA.
- Restrepo, V. R., G. G. Thompson, P. M. Mace, W. L. Gabriel, L. L. Low, A. D. MacCall, R. D. Methot, J. E. Powers, B. L. Taylor, P. R. Wade & J. F. Witzig. 1998. Technical Guidance on the Use of Precautionary Approaches to Implementing National Standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum NMFS-F/SPO-31. 54 pp.
- Southworth, M. & R. Mann. 1998. Oyster reef broodstock enhancement in the Great Wicomico River, Virginia. *J. Shellfish Res.* 17(4):1101–1114.
- Thompson, R. J., R. I. E. Newell, V. S. Kennedy & R. Mann. 1996. Reproductive processes and early development. pp. 335–370. *In*: V. S. Kennedy, R. I. E. Newell, and A. F. Eble (eds.). The Eastern Oyster, *Crassostrea virginica*. University of Maryland Sea Grant Press, College Park, Maryland. 734 pp.
- Ulanowicz, R. E. & J. H. Tuttle. 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries* 15(3): 298–306.
- Volety, A. K., F. O. Perkins, R. Mann & P. R. Hershberg. 2000. Progression of diseases caused by the oyster parasites, *Perkinsus marinus* and *Haplosporidium nelsoni*, in *Crassostrea virginica* on Constructed Intertidal Reefs. *J. Shellfish Res.* (this issue)